

Research Article

Day-Roosting Habitat of Female Long-Legged Myotis in Ponderosa Pine Forests

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Abstract

We studied use of day roosts by adult, female long-legged myotis (*Myotis volans*) in 4 watersheds dominated by ponderosa pine (*Pinus ponderosa*) forest east of the Cascade Crest in Washington and Oregon, USA, 2001–2003. To investigate maternity habitat in managed, xeric forests we radio tracked 87 bats to 195 snag roosts and 34 rock crevices totaling 842 roost-days. Bats changed roosts every 2.7 ± 0.1 (SE) days and averaged 3.5 ± 0.3 roosts per bat. Roosts were 2.0 ± 0.1 km from capture sites, and bats moved 1.4 ± 0.1 km between successive roosts. Six bats (6.9%) day-roosted in rock crevices exclusively, 9 bats (10.3%) used snags and rock crevices, and the remaining bats (82.8%) day-roosted in snags exclusively. Most snag roosts were thick-bark ponderosa pine ($n = 103$; 52.8%) or thin-bark grand fir (*Abies grandis*) and white fir (*Abies concolor*) ($n = 74$; 37.9%). Over half of all snag roosts ($n = 101$; 52%) were used by solitary bats; 28 snag roosts (14%) housed >50 bats (large-flyout roosts). Ninety-three percent of large-flyout roosts were in ponderosa pine snags. Large-flyout roosts were larger, taller, and retained more exfoliating bark and total bark than small-flyout roosts ($P < 0.05$), and small-flyout roosts were larger, taller, and retained more exfoliating bark and total bark than random snags ($P < 0.05$). Snag roosts were closer to other snags, located in areas of greater snag density, with greater snag basal area and greater basal area of snags >25 cm diameter, and were lower in elevation than random snags ($P < 0.05$). Pregnant bats divided roost-days almost evenly between thick and thin-bark snags (52.7 vs. 47.3%), whereas lactating bats roosted in thick-bark snags more often than they did in thin-bark snags (80.3 vs. 19.7%, $P < 0.0001$). Pregnant bats roosted in both upslope and riparian zones (57.5 vs. 42.5%), but lactating bats spent more days roosting upslope than in riparian zones (73.1 vs. 26.9%, $P < 0.0001$). These findings suggest that reproductive female long-legged bats choose roosts relative to their changing physiological needs. We recommend that management of forests for sustaining habitat of female long-legged myotis in the east Cascades ensure the continued availability of both thick- and thin-bark snags in early stages of decay, in both riparian and upslope positions. (JOURNAL OF WILDLIFE MANAGEMENT 70(1):207–215; 2006)

Key words

day-roost, grand fir, habitat, long-legged myotis, Pacific Northwest, ponderosa pine, radiotelemetry, riparian zone, snag, upslope, white fir, xeric forest.

Harvesting and processing timber is important to the economy of the Pacific Northwest, with Ponderosa pine (*Pinus ponderosa*) the most widely distributed pine (Whitney 1985) and the most valuable timber species in the region (Little 1980). Managed forests in the northwestern United States are under increasing pressure to provide timber while sustaining habitat for a wide array of wildlife species. Timber harvests in this region occur primarily on state forests, national forests, and private industry holdings, each subject to differing legislation. Multiple ownership has resulted in a mix of regulatory criteria associated with timber extraction in this region, including the Northwest Forest Plan, the Columbia River Basin Assessment, and the National Forest Management Act of 1976 (with amendments). In aggregate, these laws and policies suggest that 2 key elements are central to preservation of the integrity of fish and wildlife habitat in riparian forests of the Pacific Northwest. First, the provision of no-harvest buffer strips immediately adjacent to streams to protect aquatic ecosystems termed riparian management zones (RMZs). Second, retention of snags, large-diameter live trees, and downed logs within RMZs to sustain structural habitat diversity for riparian-dwelling wildlife, including insectivorous bats (U.S. Department of Agriculture and U.S. Department of the Interior 1994).

Bat activity has been recorded in riparian and upland forest habitats (Erickson 1993, Zielinski and Gellman 1999, O'Connell

et al. 2000), older forest stands (Perkins and Cross 1988, Thomas 1988, Humes et al. 1999), and both contiguous and remnant stands (Grindal et al. 1999) in western coniferous forests. However, preferred roosting sites of bats in these forests have been located mostly in upland and side-slope positions, generally outside of RMZs (Gellman and Zielinski 1996; Vonnhof and Barclay 1996, 1997; Brigham et al. 1997; Ormsbee and McComb 1998; Rabe et al. 1998; Waldien et al. 2000; Cryan et al. 2001). These findings suggest that bats primarily day-roost in upland or older-growth forests and use riparian corridors for their nightly foraging activity.

Bark and cavity-roosting bat species are closely tied to forest habitats through reliance on available roosting space in dead or damaged, standing timber, where they are protected from predators (Kunz 1982, Fenton et al. 1994). Roosts also provide protection from the weather and potential physiological benefits because of increased thermal stability (Vaughn 1987). Roost spaces that are large enough to allow clusters of bats may be of special physiological importance to females of species that form maternity colonies during the annual breeding season (Racey 1973; Tuttle 1976; Racey and Swift 1981; Kurta 1985, 1986). Because temperate zone bats spend well over half of each day inside roosts, roost choice is likely to directly influence both survival and fitness (Vonnhof and Barclay 1996).

Many bark and cavity-roosting bat species are known to use a variety of natural structures as day roosts, both within local areas and across different geographic locations (Chung-MacCoubrey

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1996, Brigham et al. 1997, Waldien et al. 2000, Weller and Zabel 2001). A consensus that roost selection is based on the physical properties of the roosting space, more so than the substrate or species of tree, has emerged from these and other studies (Mattson et al. 1996, Callahan et al. 1997, Kalcounis and Brigham 1998, Foster and Kurta 1999, Cryan et al. 2001). Roost choice is limited by roost availability at both local and larger geographic scales. However, differential selection of day roosts from those available within a local area may result from changing thermal conditions in roosts, and further, from changing physiological requirements of the bats.

At present, the U.S. Fish and Wildlife Service lists no bat species inhabiting forests of the Pacific Northwest as globally threatened or endangered. However, the long-legged myotis (*Myotis volans*) was listed as a Category 2 species and designated a "species of concern" that is in need of further study because of a poor understanding of their association with older forests (U.S. Department of Agriculture and U.S. Department of the Interior 1993). Recent studies of forest bats in Western North America have either combined data for long-legged myotis with that of other species or suffer from relatively small sample sizes (Vonhof and Barclay 1996, Frazier 1997, Ormsbee and McComb 1998, Rabe et al. 1998, Cryan et al. 2001).

Long-legged myotis exhibit variation in choice of day-roost structures in forests in Western North America. Both male and nonreproductive female long-legged myotis primarily used grand fir (*Abies grandis*) snags as day roosts in dry forests dominated by ponderosa pine, grand fir, and Douglas-fir (*Pseudotsuga menziesii*) in central Washington (Frazier 1997, Taylor 1999). In mesic forests dominated by Douglas-fir and western hemlock (*Tsuga heterophylla*) in the central Oregon Cascades, reproductive female long-legged myotis primarily used Douglas-fir snags as day roosts (Ormsbee and McComb 1998). In homogeneous ponderosa pine forests in the Southern Black Hills of South Dakota, USA, both reproductive and nonreproductive female long-legged myotis used rock crevices and ponderosa pine snags equally (Cryan et al. 2001).

Several common behaviors, such as the use of multiple roosts, reuse of roosts, and the use of multiple roosts within the same general area, have been reported for female long-legged myotis (Vonhof and Barclay 1996, Frazier 1997, Ormsbee and McComb 1998, Rabe et al. 1998, Cryan et al. 2001). Further, several habitat characteristics of day roosts of female long-legged myotis have been identified. Relative to randomly located snags, roosts of long-legged myotis are larger and taller, closer to other snags, and located in areas of greater snag density and basal area (Vonhof and Barclay 1996, Ormsbee and McComb 1998, Rabe et al. 1998, Cryan et al. 2001). Rabe et al. (1998) also found that the amount of exfoliating bark was greater for roosts of these bats than for randomly located snags in Northern Arizona. Regardless, a clear pattern of roost use in habitats within and outside RMZs by reproductive female long-legged myotis has yet to develop.

Because forest bats switch roosts frequently (Lewis 1995) and reliable data from which to assess changes in population size are difficult to acquire (Hayes 2003), studies with large sample sizes of radiotagged bats coupled with roost monitoring are needed. We designed our study to determine the structures chosen as day

roosts by female long-legged myotis in the xeric ponderosa pine-dominated forests east of the Cascade Crest in Washington and Oregon, USA. We sought to acquire sufficient sample sizes (Lacki and Baker 2003) to examine roost use by females in different stages of reproduction. Finally, we wanted to determine local and stand-level habitat characteristics that differentiated available snags from those used as maternity roosts.

Study Area

We conducted this study on the east side of the Cascade Range in Kittitas and Yakima counties in south-central Washington, and Klamath and Lake counties in south-central Oregon, USA. Andesite and basalt flows with ridge crests dissected by deep valleys characterize the physiography of the Washington study area (Franklin and Dyrness 1988). Miocene to recent basalt flows, pyroclastics, and alluvial sediments overlying fault-block mountain topography comprise the physiography of the Oregon study area. Coarse-textured, sandy soils support a ponderosa pine forest zone on the east side of the Cascades that abuts shrub-steppe habitat east of both study areas (Franklin and Dyrness 1988). Ponderosa pine dominates upland xeric habitat in southern Washington, with grand fir and Douglas-fir becoming a larger component on more mesic sites. Ponderosa pine also dominated the Oregon study area, with white fir (*Abies concolor*), western juniper (*Juniperus occidentalis*), and incense cedar (*Libocedrus decurrens*) also present. Both areas experience dry summers (<15 mm/month) and winters with heavy snowfall (Franklin and Dyrness 1988). Study areas in Washington and Oregon were ≥ 500 km apart.

We selected 2 watersheds ≥ 20 km from one another for sampling in each study area. Watersheds in Washington were situated within the Rock Creek and Oak Creek drainages on the Wenatchee National Forest. Land ownership was based on alternating township sections managed by the U.S. Forest Service and Plum Creek Timber Company. Additionally, the Washington Department of Fish and Wildlife managed several township sections in the Oak Creek drainage comprising the Oak Creek Wildlife Management Area. Capture sites and roosting sites of bats occurred along the right-hand fork of the Rock Creek drainage between 1,000 and 1,400 m and along the north and south forks of the Oak Creek drainage between 760 and 1,260 m. Oregon watersheds were situated within the Pole Creek and Sprague River drainages on the Fremont-Winema National Forest. Land ownership was interspersed parcels managed by the U.S. Forest Service, U.S. Timberlands, and the Bureau of Land Management. Capture sites and roosting sites of bats occurred in the vicinity of Pole Creek between 1,450 to 1,650 m and along small tributaries of Sprague River between 1,550 and 2,000 m.

Methods

We caught bats with mist nets placed across and around ephemeral ponds and areas of pooled water along creeks at 11 locations in each of the Rock and Pole Creek watersheds and 15 locations in each of the Oak Creek and Sprague River watersheds on 171 nights from 22 May to 17 August 2001–2003. We identified bat species, determined their age based on ossification of the epiphyseal cartilage in the finger joints (Anthony 1988), and

recorded the sex and reproductive condition of each bat. We assessed reproductive condition of female bats by noting the presence of a fetus in the abdomen (pregnant), exposed and swollen teats (lactating), exposed but not swollen teats (post-lactating), or lack of evidence of reproductive condition (non-parous; Racey 1988). We weighed bats to the nearest 0.25 g with spring scales.

We clipped fur between the scapulae and used Skin-Bond (Smith Nephew United, Largo, Florida, USA) to attach 0.48- to 0.51-g radio transmitters (Model LB-2, Holohil Systems, Ltd., Ontario, Canada) to those adult, female long-legged myotis that weighed ≥ 6.5 g. Transmitter mass averaged $6.3 \pm 0.1\%$ of the body mass of tagged bats. We used TRX-2000s receivers and 3-element Yagi antennae (Wildlife Materials, Inc., Carbondale, Illinois, USA) to locate day roosts for each radiotagged bat for the duration of the battery life of the transmitter (ca. 21 d) or until the transmitter was found detached. We radiotagged as many bats as we could follow concurrently throughout each season to assure reasonable statistical power for comparison of habitat characteristics (Lacki and Baker 2003). The Institutional Animal Care and Use Committee at the University of Kentucky (IACUC no. 00219A2001) approved all animal-handling methods used in this study.

Bats flying from the roost at dusk were counted to assess size of colonies. Count protocol consisted of arrival 15 to 30 minutes before local sunset, positioning of the observer with a view of the most probable roost exit with fading daylight as a backdrop, and counting exiting bats until darkness precluded further observation. Each roost was counted ≥ 3 times per season, and colony roosts were counted weekly. We stopped counts at a roost if no bats were seen during consecutive counts. In 2002, we also monitored 64 roosts that were first located in 2001. We classified roosts as small-flyout (< 50 bats) or large-flyout (≥ 50 bats) roosts. We did not determine the species composition of the flyouts other than that of radiotagged individuals. In 2002, we returned to each of the snag roosts located in 2001 and half of the random trees in each watershed to assess 1-year fall rates.

For each roost tree and 160 randomly located snags, we recorded geographic position and snag-centered habitat characteristics inside nested, concentric, 10- and 20-m radius plots. We identified the species and snag decay class of each tree (Hunter 1990) and determined whether the tree was topped, or contained cavities or splits. We measured snag diameter 1.5 m aboveground (diameter breast height [dbh]) and recorded percentage of slope, height of the focal tree (m), height of canopy midpoint (m), height of the nearest live tree (m), and slope aspect. We guessed percentage of canopy cover, midstory cover, branches, bark, and exfoliating bark remaining by eye. We converted percentage of bark coverage and percentage of exfoliating bark to cm^2 by multiplying by the surface area of each snag. We measured the distance to the nearest live tree ≥ 10 cm dbh, the nearest live tree \geq the focal tree in height, and the nearest available snag (i.e., ≥ 30 cm dbh and ≥ 3 m tall; sensu Ormsbee and McComb 1998, Rabe et al. 1998). We counted the number of live trees and snags ≥ 10 cm dbh within 20 m of the focal tree, and determined the basal area of live trees, snags, and large live trees and large snags (i.e., ≥ 25 cm dbh).

We indexed use, proximity, and occupancy of roosts of radiotagged bats by calculating the number of days tracked per bat, number of total roosts used per bat, distance between successive roosts, distance between capture sites and subsequent roosts, and the number of bat days per roost. We present information on movements of radiotagged bats, reuse of roosts, and use of roosts by > 1 radiotagged bat for all snag roosts and large-flyout roosts, separately. We used a *t*-test to compare the size of roosts chosen by pregnant bats with the size chosen by lactating bats using the first flyout count at a roost as data. We used a logistic regression model to assess differences among reproductive classes in the number of roost-days spent in thick-versus thin-bark snags, in snags located in riparian zones versus upslope positions, and in small-flyout versus large-flyout roosts. We grouped ponderosa pine, Douglas-fir, black cottonwood (*Populus trichocarpa*), incense cedar, and western juniper as thick-bark species, and *Abies* spp., bigleaf maple (*Acer macrophyllum*), and quaking aspen (*P. tremuloides*) as thin-bark species. We used an arcsine-transformation on all percentage data before analysis and tested snag and stand-level habitat characteristics among large-flyout roosts, small-flyout roosts, and random snags with a general linear model and subsequently separated means with Tukey's HSD ($P < 0.05$).

Results

We radiotagged 92 adult, female long-legged myotis, successfully locating roosts for 12 to 16 bats per watershed per year. We failed to detect radio signals from 5 bats. Thirty-one (35.6%) of the successfully tracked bats were pregnant, 24 (27.6%) were lactating, 9 (10.3%) were postlactating, and 23 (26.4%) were nonparous at the time of transmitter attachment. Bats were tracked for an average of 9.7 ± 1.1 (SE) days (range 1–24), used 3.6 ± 0.3 roosts (range 1–10), and changed roosts every 2.7 ± 0.2 days (range 1–20; Table 1). Radiotagged bats stayed 2.5 ± 0.3 days at their first roost, and 29.9% of all bats returned to roosts they had used previously; 41.4% of all bats used roosts first identified by tracking another radiotagged bat, and radiotagged bats reused 28.2% of all snag roosts.

Roosts were 2.0 ± 0.1 km from capture sites and bats moved 1.4 ± 0.1 km between successive roosts. Bats roosted in crevices in rock outcrops, talus slopes, or boulder fields ($n = 34$); snags ($n = 189$); and dead portions of declining trees ($n = 6$). Six bats (6.9%) day-roosted only in rock crevices, 9 (10.3%) used snags and rock crevices, and 72 bats (82.8%) only used snags. Most snag roosts were ponderosa pine ($n = 103$, 52.8%) or white and grand fir ($n = 74$, 37.9%). The remaining 18 snag roosts were Douglas-fir, black cottonwood, incense cedar, bigleaf maple, western juniper, and quaking aspen.

Flyout Counts

Counts at known day-roost snags of long-legged myotis ($n = 495$) revealed that all roosts in ponderosa pine and nearly all roosts in *Abies* spp. snags were under exfoliating bark. Roosts in other tree species were in hollows, splits, or other damaged portions of the snag. Most snag roosts ($n = 101$, 51.8%) were used by solitary bats; 66 (33.8%) housed a maximum of between 2 and 49 bats, 13 (6.7%) housed between 50 and 199 bats, and 15 (7.7%) housed ≥ 200 bats. Among the largest roosts, 4 housed at least 345 bats,

Table 1. Summary of radiotracking data (mean \pm SE) for adult, female long-legged myotis by study area and watershed on the Wenatchee National Forest in Washington, USA, 2001 and 2002, and the Fremont–Winema National Forest in Oregon, USA, 2003.

Study area watershed	No. of bats	No. of roosts	No. of days tracked	No. of days tracked/bat	Roosts/bat	Distance (km) to		
						Capture	Previous roost	Mean no. of days/roost
Washington								
Rock Creek	35	86	439	12.5 \pm 1.2	3.7 \pm 0.3	1.5 \pm 0.1	1.2 \pm 0.1	3.4 \pm 0.3
Oak Creek	25	70	222	8.9 \pm 1.3	3.6 \pm 0.4	2.0 \pm 0.2	1.0 \pm 0.2	2.5 \pm 0.3
Oregon								
Pole Creek	15	41	95	6.3 \pm 1.1	3.4 \pm 0.6	2.4 \pm 0.4	1.9 \pm 0.4	1.9 \pm 0.2
Sprague River	12	32	86	7.2 \pm 1.1	3.5 \pm 0.6	2.5 \pm 0.4	1.9 \pm 0.5	2.0 \pm 0.2
Total	87	229	842	9.7 \pm 1.1	3.6 \pm 0.3	2.0 \pm 0.1	1.4 \pm 0.1	2.7 \pm 0.2

and 1 was a ponderosa pine that housed 459 bats on 8 July 2003 in the Sprague River, Oregon, USA, watershed.

Forty-six (62.2%) *Abies* spp. snag roosts and 40.8% of ponderosa pine snag roosts were used by solitary bats. During nearly half (47.3%) of all flyout counts, we noted ≥ 1 bat approaching, and often circling, the focal snag from other areas at twilight. Twenty-six (92.9%) snag roosts that housed ≥ 50 bats (i.e., large-flyout roosts) were ponderosa pine, a thick-bark species at maturity (i.e., ca. 40 cm dbh). The only large-flyout roost in a thin-bark species was a white fir used by 4 (26.7%) different radiotagged bats in the Pole Creek, Oregon, USA, watershed in 2003. The size of the first flyout count was greater for thick-bark species than for thin-bark species (44.2 ± 8.2 vs. 3.6 ± 1.2 bats, $t = 4.9$, $df = 123$, $P < 0.0001$).

Roost-Use Behaviors

Twelve (85.7%) large-flyout roosts were located in Washington in 2001, but only 2 additional large-flyout roosts were located using 28 radiotagged bats in the same area in 2002. Half of the large-flyout roosts located in 2001 were used the next season, and a third continued to house large numbers of bats in 2002. Flyout counts at 12 (36.4%) snag roosts located in 2001, but not used by radiotagged bats in 2002, revealed use in 2002 despite the absence of any radiotagged bats. Fifteen of 66 (22.7%) snag roosts and 21 of 50 (42%) randomly located snags in 2001 had fallen when relocated in 2002.

Half of the 28 large-flyout snag roosts were reused by radiotagged bats during the study. All but 2 snag roosts reused by subsequently radiotracked bats became large-flyout roosts later in the study. Monitoring revealed that all but 5 large-flyout roosts were abandoned by colonies within 9–20 days of discovery. We observed evidence of colony movements, en masse, among large-flyout roosts within watersheds. On 13 occasions, when radiotagged bats moved from a large-flyout roost to another roost, flyout counts revealed a colony size in the new roost similar to that previously counted at the initial roost. The initial roost, in turn, then supported only a few bats.

Influences of Reproductive Condition

Although bats used snags of 9 tree species, they roosted in ponderosa pine snags for 54.9%, and *Abies* spp. snags for 36.9% of the 732 roost-days that we confirmed a radiotagged bat to be present in a snag (Table 2). Bats spent 63.1% of all roost-days in thick-bark snag roosts. When bats were pregnant at the time of

transmitter attachment, total roost-days were divided almost evenly between thick and thin-bark snags (52.7 vs. 47.3%), but when bats were lactating or postlactating at the time of transmitter attachment, these percentages changed to 80.3 vs. 19.7 % and 68.8 and 31.2%, respectively. Pregnant and nonparous bats divided roost-days almost evenly between snags in upslope positions and those in riparian zones (57.5 vs. 42.5% and 56.5 vs. 43.5%, respectively), but lactating and postlactating bats spent more days roosting upslope than in riparian zones (73.1 vs. 26.9% and 86.2 vs. 13.8%, respectively).

Logistic regression indicated that bat use of thick- vs. thin-bark, riparian versus upslope, and small-flyout versus large-flyout snag roosts was nonrandom ($\chi^2 = 23.5$, $df = 2$, $P < 0.0007$). Bats spent more roost days than expected in thin-bark snags when pregnant and more roost days than expected in thick-bark snags after parturition ($\chi^2 = 33.8$, $df = 2$, $P < 0.0001$). Bats also spent more roost days than expected in snags in riparian zones when pregnant and more roost days in snags in upslope positions than expected after parturition ($\chi^2 = 21.4$, $df = 2$, $P < 0.0001$). Lastly, bats spent more days in small-flyout roosts than expected when pregnant and more days in large-flyout roosts than expected after parturition ($\chi^2 = 22.8$, $d.f. = 2$, $P < 0.0001$).

Snag Characteristics among Flyout Classes

Large-flyout roosts were larger in dbh (82.3 ± 3.6 cm, $n = 28$) than small-flyout roosts (60.9 ± 1.9 cm, $n = 164$), which were larger than random snags (54.0 ± 1.7 cm, $n = 160$; Table 3). Large-flyout roosts were also taller (31.5 ± 2.3 m) than small-flyout roosts (26.7 ± 0.6 m), which were taller than random snags (14.7 ± 0.7 m). Large-flyout roosts retained more total bark ($1,648.5 \pm 178.3$ cm²) and exfoliating bark (561.4 ± 79.8 cm²) than small-flyout roosts, which retained more total bark ($1,290.9 \pm 69.5$ cm² vs. 590.7 ± 53.8 cm²) and exfoliating bark (360.8 ± 28.8 cm² vs. 56.8 ± 7.1 cm²) than random snags. The difference between snag height and canopy height was similar for large-flyout roosts (7.7 ± 2.1 m) and small-flyout roosts (4.6 ± 0.7 m) but greater for roosts than random snags (-2.0 ± 0.7 m). Distance to the nearest live tree did not differ among flyout classes and random snags. Small-flyout roosts had taller nearest live trees (18.9 ± 0.7 m) than random snags (15.8 ± 0.6 m). Distance to the nearest tree taller than the roost tree did not differ among flyout classes and random snags. Large- and small-flyout roosts

Table 2. Total roost-days, roost periods, and mean \pm SE roost-days per roost period for radiotagged, adult, female long-legged myotis by bark type, tree species, and reproductive condition class at capture on the Okanogan–Wenatchee National Forest, Washington, USA, in 2001 and 2002, and the Fremont–Winema National Forest, Oregon, USA, in 2003.

Bark type	Roost-days	Roost periods	Reproductive condition at capture			
			Pregnant	Lactating	Postlactating	Nonparous
Thick Bark						
Mean \pm SE			2.4 \pm 0.3	2.7 \pm 0.4	2.6 \pm 0.4	3.3 \pm 0.6
Total roost days (%)	462 (63.1)	172 (63.5)	145 (52.7)	155 (80.3)	55 (68.7)	107 (58.2)
Thin Bark						
Mean \pm SE			3.3 \pm 0.4	1.9 \pm 0.2	2.5 \pm 0.9	2.6 \pm 0.5
Total roost days (%)	270 (36.9)	99 (36.5)	130 (47.3)	38 (19.7)	25 (31.3)	77 (41.8)

were nearer to other snags (22.1 ± 4.3 and 14.8 ± 1.6 m) than random snags (41.3 ± 3.3 m).

Stand Characteristics among Flyout Classes

Live tree density was greater in stands containing small-flyout roosts (291.7 ± 17.5 trees/ha) than for random snags (202.3 ± 12.8 trees/ha; Table 3). Large-flyout and small-flyout roosts were located in stands of greater snag density (41.2 ± 15.4 and 42.7 ± 3.6 snags/ha) than random snags (16.6 ± 1.8 snags/ha). Live tree basal area did not differ in stands among flyout classes and random snags. Snag basal area was greater for stands containing large-flyout and small-flyout roosts than for random snags (11.1 ± 2.5 and 11.5 ± 0.8 m²/ha vs. 9.4 ± 0.8 m²/ha). Basal area of large-diameter, live trees was greater for small-flyout roosts (11.5 ± 0.8 m²/ha) than for random snags (9.4 ± 0.8 m²/ha). Basal area of large snags was greater surrounding large-flyout and small-flyout roosts (3.0 ± 0.7 and 4.3 ± 0.4 m²/ha, respectively) than surrounding random snags (1.4 ± 0.2 m²/ha). Large-flyout and small-flyout roosts were lower in elevation than random snags ($1,262.7 \pm 68.2$ and $1,216.8 \pm 25.2$ m asl vs. $1,324.7 \pm 25.3$ m above sea level [asl], respectively).

Discussion

Female long-legged myotis switched roosts every 2 to 4 days on average and primarily roosted under loose bark of snags, consistent with other studies of this species (Vonhof and Barclay 1996, Frazier 1997, Ormsbee and McComb 1998, Rabe et al. 1998, Cryan et al. 2001). This behavior and the extensive reuse of roosts in Washington and Oregon suggest both familiarity with, and temporal preference for, multiple roosts by adult, female long-legged myotis. The range of distances between capture sites and successive roosts of female long-legged myotis in this and other studies suggests that females generally roost within relatively short reaches of watersheds (i.e., 1–3 km; Rabe et al. 1998, Cryan et al. 2001). The observed behavior of bats approaching and circling known snag roosts at twilight also suggests familiarity by individual bats with snag roosts used by other bats. The use of distinct patches of habitat by forest bats supports the contention that tree-roosting species are dependent on specific roosting areas (Betts 1996, Ormsbee 1996, Sasse and Pekins 1996, Cryan et al. 2001).

Flyouts at roosts that housed large numbers of bats differed from others in behavioral aspects, which we hypothesize are associated with the demands of lactation and the rearing of pups. Many bats remained near large-flyout roosts during counts as opposed to a

nearly complete departure noted at small-flyout roosts. Several bats returned and reentered large-flyout roosts during counts, suggestive of mothers nursing pups. At large-flyout roosts, but not small-flyout roosts, bats repeatedly approached within centimeters of the roost entrance, sometimes landing briefly, only to immediately fly away. Individual bats often repeated this behavior dozens of times before landing and reentering the roost or simply flying away. Others have noted this behavior and hypothesized that mothers may be attempting to coax pups to fly or that these observations may be early flights of newly volant young (P. Ormsbee, USFS, personal communalization).

Radiotagged female long-legged myotis rarely were located in the same roost together, consistent with other studies (Ormsbee and McComb 1998, Rabe et al. 1998, Cryan et al. 2001). Regardless, the high levels of reuse of roosts by bats (Frazier 1997, Rabe et al. 1998) and the use of the same roost by radiotagged bats at different times indicate the importance of selected roosts within watersheds. Flyout counts of large numbers of bats indicate a high level of importance of such snag roosts, and confirmed reuse of such snags between years is further evidence of their importance, regardless of their ephemerality (Barclay and Brigham 2001). Moreover, verification of large numbers of bats in successive roosts, concurrent with discontinued use of roosts that previously housed large numbers of bats, indicates that multiple roosts capable of housing large numbers of bats are required by colonies of long-legged myotis at the watershed scale.

Use of rock crevices as day-roosts by long-legged myotis has been reported, but the extent to which such roosts are used varies widely (Ormsbee and McComb 1998, Cryan et al. 2001), with no evidence of use of rock crevices by this bat in northern Arizona (Rabe et al. 1998). Rock crevices represented only 14.8% of all roosts in our study and were used by a minority (17.2%) of radiotagged bats. Management for rock habitat is relatively uncomplicated, and might be limited to simply minimizing human disturbance in areas known to be used as day-roosting habitat by long-legged myotis.

In our study, extensive use of ponderosa pine snags as day-roosts by female long-legged myotis was consistent with behavior of bats in northern Arizona, where all lactating, female long-legged myotis day-roosted in ponderosa pine snags (Rabe et al. 1998). Further, in the Black Hills of South Dakota, 66.7% of female long-legged myotis day-roosted in ponderosa pine snags (Cryan et al. 2001). Consistent among these studies and ours are landscapes primarily comprised of xeric habitat. On more mesic sites, female

Table 3. Habitat data as means \pm SE for large-flyout roosts (i.e., ≥ 50 bats); small-flyout roosts (< 50 bats); and randomly selected snags in Washington, USA, in 2001 and 2002, and in Oregon, USA, in 2003.^a

Habitat variable	Large-flyout roosts <i>n</i> = 28 mean (SE) ^b	Small-flyout roosts <i>n</i> = 164 mean (SE) ^b	Random snags <i>n</i> = 160 mean (SE) ^b	Parameter estimate	SE
Snag dbh (cm)	82.3 (3.6) ^a	60.9 (1.9) ^b	54.0 (1.7) ^c	0.0078	0.0014
Snag height (m)	31.5 (2.3) ^a	26.7 (0.6) ^b	14.7 (0.7) ^c	0.0338	0.0025
Snag decay class (1–9) ^c	4.2 (0.1)	3.9 (0.1)	4.3 (0.1)	–0.0601	0.0284
Snag bark cover (cm ²)	1,649 (178.3) ^a	1,291 (69.5) ^a	591 (53.8) ^b	0.0003	0.0001
Snag exfoliating bark cover (cm ²)	561 (79.8) ^a	361 (28.8) ^b	56.8 (7.1) ^c	0.0009	0.0001
Difference between roost tree height and canopy height (m)	7.7 (2.1) ^a	4.6 (0.7) ^a	–2.0 (0.7) ^b	0.0239	0.0033
Canopy cover (%)	22.1 (3.9)	31.2 (1.9)	28.5 (1.7)	–0.0240	0.1271
Distance to nearest live tree (m)	6.3 (0.9)	4.2 (0.2)	4.8 (0.5)	0.0025	0.0065
Height of nearest live tree (m)	19.0 (1.9) ^{ab}	18.9 (0.7) ^a	15.8 (0.6) ^b	0.0121	0.0038
Distance to nearest tree taller than roost tree (m)	20.5 (3.7)	14.2 (1.3)	11.7 (1.6)	0.0039	0.0018
Distance to nearest available snag (m) ^d	22.1 (4.3) ^a	14.8 (1.6) ^a	41.3 (3.3) ^b	–0.0059	0.0010
Live tree density (trees/ha)	249.7 (46.4) ^{ab}	291.7 (17.5) ^a	202.3 (12.8) ^b	0.0005	0.0002
Snag density (trees/ha)	41.2 (15.4) ^a	42.7 (3.6) ^a	16.6 (1.8) ^b	0.0038	0.0007
Live basal area (m ² /ha)	18.6 (3.0)	21.2 (1.0)	19.3 (1.0)	0.0016	0.0026
Snag basal area (m ² /ha)	4.6 (0.7) ^{ab}	6.5 (0.6) ^a	2.3 (0.2) ^b	0.0310	0.0057
Large (≥ 25 cm) live tree basal area (m ² /ha)	11.1 (2.5)	11.5 (0.8)	9.4 (0.8)	0.0054	0.0033
Large (≥ 25 cm) snag basal area (m ² /ha)	3.0 (0.7) ^{ab}	4.3 (0.4) ^a	1.4 (0.2) ^b	0.0411	0.0079
Slope (%)	31.2 (4.9)	26.7 (2.0)	25.6 (1.7)	–0.0001	0.0004
Elevation (m asl)	1,263 (68.2) ^a	1,217 (25.2) ^a	1,325 (25.3) ^b	–0.0002	0.0001

^a dbh, diameter at breast height; asl, above sea level.

^b Means with common superscripted letters within rows are not significantly different ($P > 0.05$).

^c Sensu Hunter 1990.

^d Available snags considered were those > 3 m tall and between 30 and 200 cm dbh (sensu Ormsbee and McComb 1998).

long-legged myotis have been observed using a wider range of tree species as roosting sites, with an emphasis on Douglas-fir (Ormsbee and McComb 1998). We found grand fir and white fir to be the most frequently used day-roosting structures for solitary females in Washington and Oregon. Use of *Abies* spp. snags as day-roosts by both male and female long-legged myotis has been observed in east-central Washington (Frazier 1997) and in south-central Washington (Taylor 1999). The extensive use (37.9% of all snag roosts) of snags of *Abies* spp. as day-roosts by long-legged myotis, suggests their importance to the roosting ecology of long-legged myotis in forests on the east side of the Cascade Range.

The propensity for female long-legged myotis to select larger, taller snags that extend further into or above the local canopy (Ormsbee and McComb 1998), that are farther from taller trees (Rabe et al. 1998), and that occur in areas of lower canopy cover (Vonhof and Barclay 1996) relative to randomly available snags has been previously observed. In our study, distance to the nearest tree taller than the focal snag was greater for large-flyout roosts than for random snags, and the difference between roost tree and canopy height was greater for roosts than for random snags. These local habitat characteristics may facilitate the ease with which long-legged myotis locate roosts from the air (Bakken and Kunz 1988) or may provide a more favorable thermal environment for raising young (Vonhof and Barclay 1996, Ormsbee and McComb 1998). The latter explanation has received attention because it is

intuitive that snags, or portions thereof, exposed to sunlight during daylight hours will acquire more heat during the day than those shaded by foliage (Geiger 1957, Ormsbee and McComb 1998). Whether they extend above the local canopy or not, tall and large-diameter snags also might be selected by female long-legged myotis for day-roosting because, at the same ambient temperature, larger objects retain more thermal energy for longer periods of time than do smaller objects (Giancoli 1985).

As snags decay and bark exfoliates, spaces under plates of bark are likely to develop over a wide range of snag conditions and species. Preference for snags in earlier-to-intermediate stages of decay, when more bark remains, has been reported (Vonhof and Barclay 1996, Betts 1998, Crampton and Barclay 1998, Ormsbee and McComb 1998, Waldien et al 2000, Barclay and Brigham 2001). In our study, both total bark remaining and exfoliating bark remaining, characteristics that are more ephemeral than the snag itself, differed among large- and small-flyout roosts and random snags. Thus, it appears that for day-roosting long-legged myotis, an important aspect of the process of snag decay in *Abies* spp. and ponderosa pine is the amount of exfoliating bark (Rabe et al. 1998). As bark exfoliates spaces are created between the bole of the tree and the cracked and separating plates of bark. Typically, any single such space is relatively small on snags of *Abies* spp.; however, far larger spaces for roosting are created by this process on ponderosa pine snags. This difference in physical structure is likely the more important factor, as opposed to that of tree species,

in roost selection by bats (Mattson et al. 1996, Callahan et al. 1997, Kalcounis and Brigham 1998, Foster and Kurta 1999, Cryan et al. 2001). We found increased use of thick-bark snags during lactation and suggest that changing physiologic needs may influence roost choice by reproductive females. If thick-bark snags provide more stable thermal environments than thin-bark snags, reproductive females may improve the survival of their pups by choosing such roosts to shelter them during foraging bouts.

As did Rabe et al. (1998), we noted occasions when flyout counts at roosts that had previously housed large numbers of bats decreased markedly in conjunction with the sloughing of a large plate of bark. Roosts in ponderosa pine were often under large plates of bark that encompassed the entire diameter of the snag in Arizona (Rabe et al. 1998), and 26 of 28 large-flyout roosts were under large plates of bark in the present study. Thus, we suggest that this physical characteristic is primarily responsible for the observed use of ponderosa pine snags by colonies of long-legged myotis. Greater amounts of total bark and exfoliating bark on snags used as day-roosts relative to that of random snags suggests the importance of this habitat characteristic to the roosting ecology of both solitary and colonial roosting female long-legged myotis.

The wider habitat gestalt described by several other snag-centered habitat characteristics suggests selection by bats for older, possibly neglected forest patches. Greater live-tree density around snag roosts than around random snags has been suggested to result from forest regeneration in canopy gaps around snag roosts (Rabe et al. 1998). Greater distances between roosts and taller trees, and greater basal area of large diameter live trees around roosts than random snags, suggest that snag roosts may be remnants from prior rotations as has been previously noted for female long-legged myotis (Rabe et al. 1998). These observations indicate extensive use of remnant, inaccessible, or otherwise overlooked forest patches by bats. Lastly, 4 characteristics that might be expected to be higher in less-recently disturbed forest patches, such as proximity to other snags >30 cm dbh and >3 m tall, greater snag density, and greater snag and large snag basal area, were also associated with roosts and not random snags (Vonhof and Barclay 1996, Rabe et al. 1998, Cryan et al. 2001). The ephemeral nature of snag roosts and the movement by colonies of bats among several snags within seasons indicate that tree-roosting bats require areas of high snag density, perhaps more so than cavity-nesting birds (Rabe et al. 1998).

Snag roosts used by female long-legged myotis were situated at lower elevations than random snags in Washington and Oregon, consistent with data for this species in northern Arizona (Rabe et al. 1998). It seems intuitive that animals associated with riparian habitat for drinking and foraging will also use habitats at lower elevations than randomly available habitats in the landscape to minimize foraging costs. However, Ormsbee and McComb (1998) found that female long-legged myotis generally roosted in upland habitats on the mesic, west side of the Cascades. On the xeric, east side of the Cascades, we found that females increasingly used roosts upslope and outside of RMZs with the onset of lactation. If upslope snags receive greater solar energy than those located in riparian zones, our findings may be further evidence

that reproductive females choose roosts relative to their physiologic condition.

Management Implications

Reproductive female long-legged myotis consistently used several roosts during the relatively short time that researchers were able to track them (Vonhof and Barclay 1996, Ormsbee and McComb 1998, Rabe et al. 1998, Cryan et al. 2001). Frequent roost-switching and the ephemeral nature of bark roosts suggest that bark-roosting bats may require a greater number of suitable snags than currently thought to be sufficient as habitat for cavity-nesting forest birds (Rabe et al. 1998). Bats used larger snags than available across a wide range of landscapes (Vonhof and Barclay 1996, Ormsbee and McComb 1998, Rabe et al. 1998, Cryan et al. 2001). Thus, we suggest that snags retained as potential bat roost habitat should be large in diameter (e.g., > 60 cm dbh).

Lack of historical data regarding bat use of bark roosts, combined with a relative certainty that the existing snag distribution among riparian zones, side slopes, and uplands differs from presettlement conditions, complicates analyses of current patterns of roost use. Presettlement snag densities ranged from 14.5 to 34.6 snags per hectare in east Cascade ponderosa pine forests with live basal areas similar to those measured in this study (Harrod et al. 1998; Table 3). Interestingly, randomly located snags in this study occurred in stands with snag densities at the low end of this range, and roost snags occurred in stands with snag densities at 121% of the high end of the historical range. Therefore, we suggest that forest management prescriptions target and set aside large-diameter snags surrounded by snag densities of ≥ 40 snags per hectare in snag management efforts directed toward conservation of bat-roosting habitat. Further, because female long-legged myotis made extensive use of snags across all landscape positions, with differential use of riparian and upslope positions between pregnancy and lactation, we suggest that pockets of bat habitat be distributed across all landscape positions.

Our results support suggestions by Rabe et al. (1998) for the management of xeric ponderosa pine forests to sustain roosting habitat for bats, including thinning of young stands to expedite recruitment of large trees that are then allowed to die in place, the preservation of all existing large snags, and the killing of large ponderosa pines where large snags are deficient. Additionally, we agree that a more natural fire regime could promote future recruitment of large snags by killing large senescent trees (Rabe et al. 1998), although data are needed to confirm this possibility. Assuming the pattern of roost choice recorded in this study facilitates the reproductive success of female long-legged myotis, forest management prescriptions should provide for large snags with exfoliating bark across all landscape positions and in perpetuity. Lastly, a buffer zone should be created around snags known to house large colonies of bats despite the current lack of data on an optimal buffer radius for bats.

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